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**A REVISION OF THE NORTH AMERICAN SPECIES OF THE GENUS  
HELLUOMORPHOIDES BALL, 1951<sup>1</sup>**

(COLEOPTERA, CARABIDAE, HELLUONINI)

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INTRODUCTION

This paper is intended to elucidate the taxonomic status of the named forms of North American *Helluomorphoides*. This is the first revision of this group since the publication of Le Conte's "Synoptic Tables" (1879). The only forms of this predominantly Neotropical genus included in this study are those which enter or are endemic in continental United States. A revision of the entire genus is precluded by the paucity of Neotropical material in collections.

I am indebted to the following entomologists for their cooperation in this study, particularly for the loan of material: Dr. Henry Dietrich, Cornell University; Dr. P. J. Darlington, Jr., Museum of Comparative Zoology; Dr. R. H. Beamer, University of Kansas; Dr. Howard E. Evans, formerly of Kansas State University; Dr. Mont A. Cazier, American Museum of Natural History; Dr. J. Manson Valentine, Alabama Museum of Natural History; Dr. A. B. Champlain, formerly of the Bureau of Plant Industry, Harrisburg, Pa.; Mr. Hugh B. Leech, California Academy of Sciences. In addition, I take this opportunity to thank Dr. V. S. L. Pate, formerly of Cornell University, Dr. Ralph L. Chermock, University of Alabama, and Mr. Barry D. Valentine, Cambridge, Massachusetts, for their numerous valuable criticisms and suggestions. Finally, I thank Drs. P. J. Darlington, Jr., Museum of Comparative Zoology, and Ross H. Arnett, Jr., formerly of the United States National Museum, for their cooperation and assistance during my two visits to each institution.

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## TAXONOMIC TREATMENT

As the material studied consisted of dead specimens, it was necessary to base taxonomic conclusions on morphological and distributional data, using the following criteria. Two similar forms were considered as distinct species if their geographical ranges overlapped, and if they exhibited no intergradation in at least one diagnostic morphological character in the area where they were sympatric. If such intergradation was found they were considered to be conspecific. If two forms were completely allopatric, as evidenced by available material, the criterion was the structure of the genitalia. If these were identical, the population samples were considered to be conspecific. If the genitalia were different the samples were considered to represent distinct species.

The material studied consisted of 792 specimens which were either borrowed from the museums noted in the acknowledgements, or collected by me. The range of variation of various structures was studied either by direct observation, or by actual measurement. Measurements were made with an ocular micrometer, in a binocular microscope. These were used to determine the following ratios:

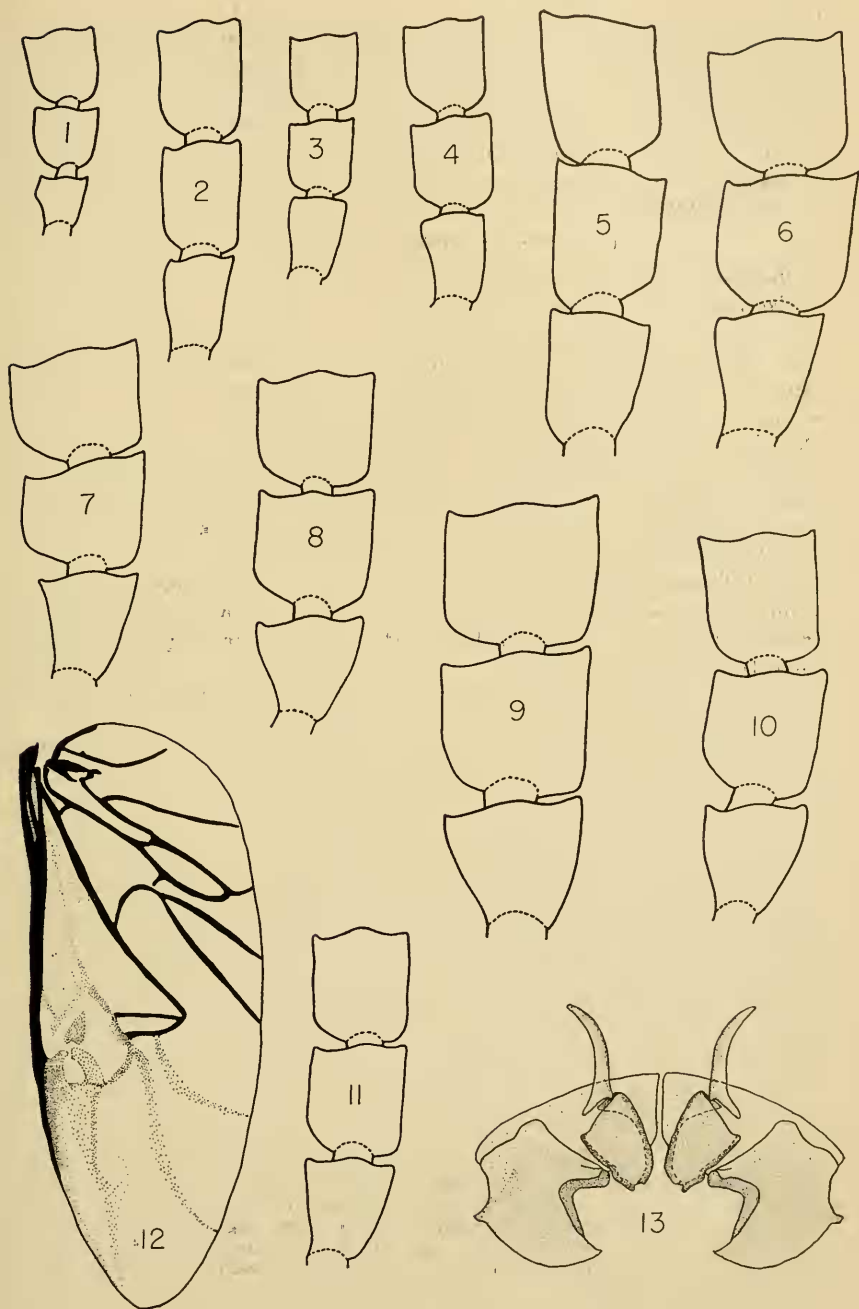
1. Antennal segment 6-L/W: median length/median width;
2. W.pn/W.ant.seg.6: maximum width of pronotum/width of antennal segment 6;
3. L.pn/W.base: median length of pronotum/width of pronotum at base.

Total length is the sum of the lengths of the head, pronotum (along the median line), and elytra (along the suture). Width is the maximum width of both elytra taken together. In the species descriptions, each numerical character is presented as a series of three figures, the middle one representing the average value, and the other two the extremes (i.e. L.pn/W.base—1.22-1.24-1.30).

The shape of the pronotum varies somewhat intraspecifically, but when coupled with other characters it is quite useful in delimiting species and subspecies. The ratio of antennal segment 6 can be taken to represent the proportions of segments 5-10 for each of the forms studied, as these segments are essentially the same in relative proportions. The arrangement of the elytral punctures is clearest in the discal region of striae 1-6. Laterally and apically the punctation is usually more confused. The term "biseriate" as used in this paper

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Fig. 1, right antenna, segments 4, 5, and 6, of *H. nigripennis*, Jamesburg, N. J.; Fig. 2, same of *H. ferrugineus*, Boerne, Tex.; fig. 3, same of *H. ferrugineus*, Brownsville, Tex.; fig. 4, same of *H. ferrugineus*, Stockton Pass, Pinaleno Mts., Ariz.; fig. 5, same of *H. praeustus floridanus*, "Fla."; fig. 6, same of *H. praeustus praeustus*, Grand Bay, Mobile Co., Ala.; fig. 7, same of *H. praeustus bicolor*, "Kansas"; fig. 8, same of *H. texanus*, Riviera Beach, Tex.; fig. 9, same of *H. clairvillei*, Ocala, Fla.; fig. 10, same of *H. latitarsis*, Parral, Chihuahua, Mex.; fig. 11, same of *H. papago*, Baboquivari Mts., Ariz.; fig. 12, left metathoracic wing of *H. ferrugineus*, Boerne, Tex.; fig. 13, female retractile plates, ventral aspect, of *H. ferrugineus*, Boerne, Tex.



means that the punctures are arranged approximately in two rows in striae 1-6; "triseriate" means that the punctures in these striae are approximately in three rows. It must be emphasized that these terms are not to be taken to be literally accurate but rather to express general impressions, because often the punctures are about but not quite bi- or triseriate in arrangement. For this reason it was finally deemed inadvisable to place much importance on intraspecific variation in elytral punctation.

Genus *Helluomorphoides* Ball, 1951

*Helluomorpha* Castelnau, 1834: 52, [in part].

*Helluomorphoides* Ball, 1951: 135-136.

Type of genus: *Helluomorpha texana* Le Conte, 1853: 374.

The name *Helluomorphoides* was proposed because the original name, *Helluomorpha* Castelnau, 1834, was apparently not available for this group of insects. See Ball (1951) for details.

*Diagnosis*.—Head always with two supra-orbital setigerous punctures on each side; labrum evenly rounded, without an anterior median triangular prominence; ligula not fringed with setae, tooth of submentum triangular, not long and pointed; anterior femora without antebasal protuberances; wings fully developed; distribution North and South America.

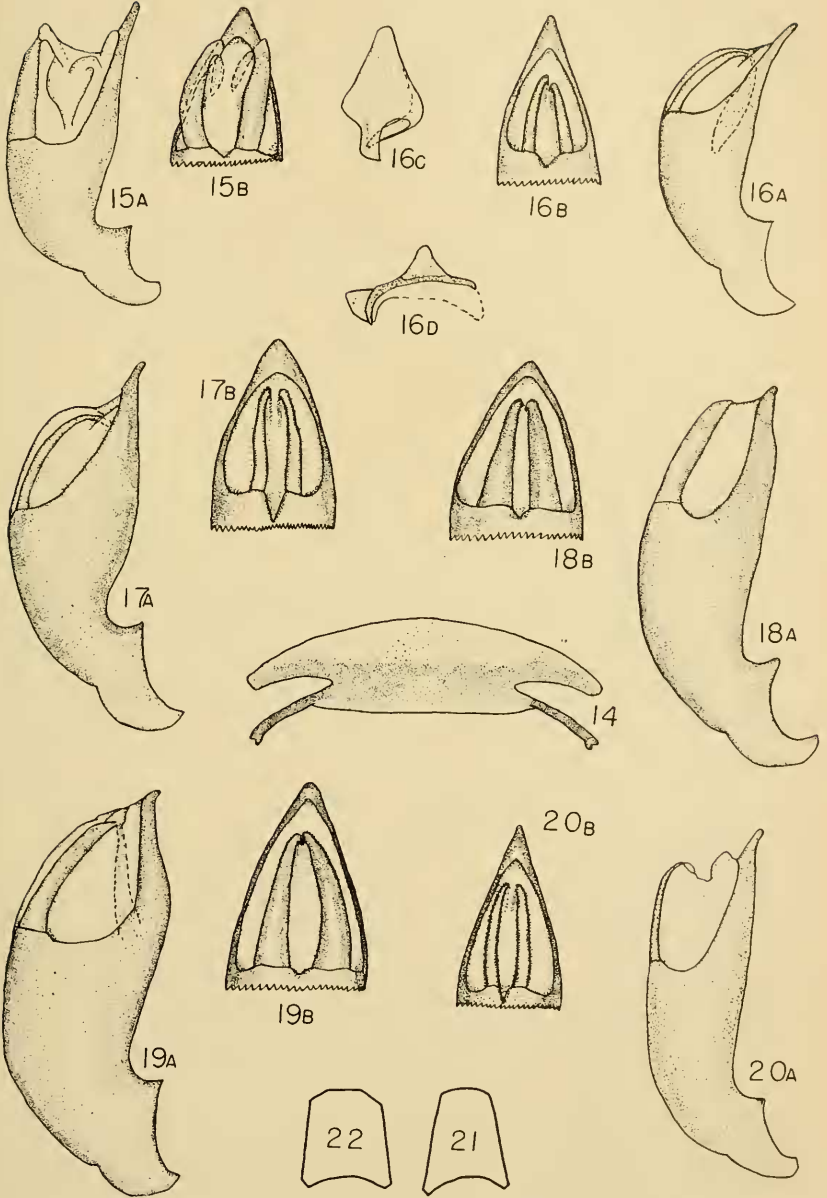
The following generic description includes characters shared in common by those members of *Helluomorphoides* treated in this study. It seemed best to record them here, rather than repeating them in the description of each species.

*Description*.—Species of moderate size, depressed; punctate in varying degrees, punctures bearing short, pale yellow hairs.

*Head* approximately quadrate in outline, generally densely but finely punctate. Antennae clavate; segments 1-3 cylindrical, longer than wide, densely but finely punctate, punctures in approximately longitudinal rows on scape, in circular rows on pedicel, and scattered on segment 3, surface not granulate; scape as long as pedicel plus segment 3; segment 4 more or less compressed, generally widening somewhat from base to apex, surface not granulate, finely and irregularly punctate; segments 5-10 compressed (see Figs. 1-11), basal angles of each segment rounded, apical angles sharp, apical margin undulant, surface granulate-pubescent with exception of a glabrous triangular area in center of broad surface of each segment, base of this triangle at base of segment, apex not quite reaching apex of segment, impunctate except as noted under species descriptions, a series of long slender setae along apical margin of each segment; segment 11 distinctly longer

Fig. 14, tenth tergite, female, of *H. ferrugineus*, Boerne, Tex. Figs. 15, a & b, median lobe of *H. nigripennis*, So. Car.; a, left lateral aspect; b, apical portion, dorsal aspect. Figs. 16, a to d, male genitalia of *H. ferrugineus*, Stockton Pass, Pinaleno Mts., Ariz.; a, median lobe, left lateral aspect; b, median lobe, apical portion, dorsal aspect; c, left lateral lobe; d, right lateral lobe. Figs. 17, a & b, median lobe of *H. p. praevustus*; a, left lateral aspect; b, apical portion, dorsal aspect. Figs. 18, a & b, same of *H. texanus*, Coneau, Tex.; figs. 19, a & b, same of *H. latitarsis*, Baboquivari Mts., Ariz.; figs. 20, a & b, same of *H. papago*, Fort Grant, Ariz.; fig. 21, hind tarsus, seg. 3, of *H. texanus*, Devera, Tex.; fig. 22, same of *H. latitarsis*, "Arizona."





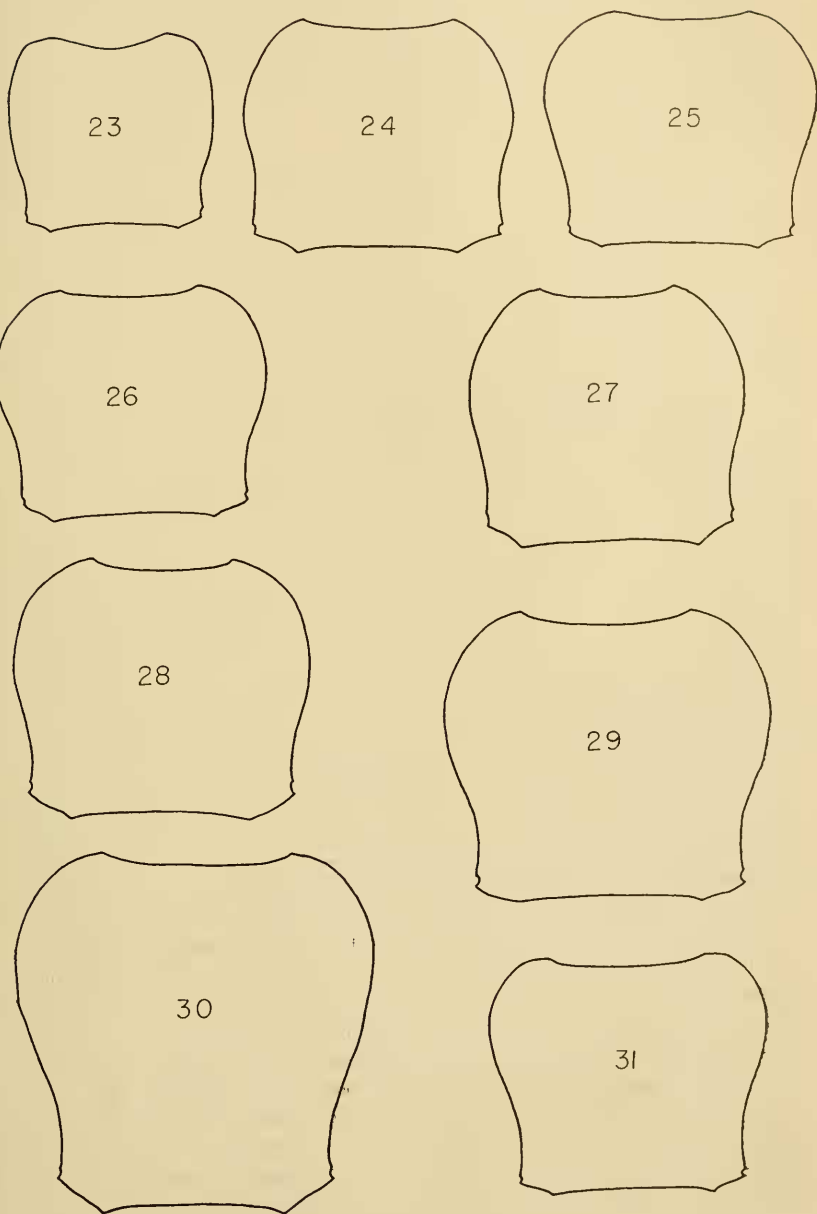
than wide and generally longer than any other segment, tapering to a blunt, rounded tip, triangular depression long and slender, extending for approximately  $\frac{3}{4}$  the length of the segment, lateral areas as in segments 5-10, apical setae lacking. Eyes large and prominent, except as noted in species descriptions. Frontal grooves of head broad and shallow. Genae with a single row of punctures bordering ventral margin of eyes, and a cluster of punctures along inner margin bordering gula. Clypeus narrow, transverse, anterior margin slightly concave, and lateral margins slightly convex, densely punctate along anterior margin, very sparsely and finely so over rest of surface. Labrum large, completely concealing mandibles, a single row of punctures varying in number from 5 to 9, bordering the generally arcuate anterior margin. Mandibles stout, arcuate, acute at tip. Maxillary palpi stout, terminal segment more or less depressed and truncate at tip. Labial palpi shorter and not as broad as segments of maxillary palpi, terminal segment fusiform, and truncate at tip, penultimate segment bisetose. Ligula large, prominent; paraglossae reduced, adherent to sides of ligula. Submentum emarginate, with strong acute median tooth as long as lateral lobes. Gula impunctate.

*Thorax.* Pronotum as in Figs. 23-31; postero-lateral depressions broad and deep, generally densely punctate; propleurae sparsely and coarsely punctate; prosternum punctate at base, impunctate at apex; metasternum punctate along lateral margins, impunctate medially; metepisterna long and slender, coarsely and densely punctate. Legs of average length, femora and tibiae flattened, finely punctate; tarsal segment 4 emarginate, anterior tarsi the same in males as in females. Elytra widening somewhat from base to apex, apical margins truncate, humeri rounded, intervals in general only slightly elevated, the seventh generally obscure. Metathoracic wings fully developed (see Fig. 12), venation constant. Venter finely and densely punctate. Male genitalia with median lobe as in Figs. 15-20. Internal sac a large shapeless mass, devoid of spines or plates. Right lateral lobe as in Fig. 16d. Left lateral lobe as in Fig. 16e. Female retractile plates as in Fig. 13; tenth tergite as in Fig. 14.

#### KEY TO THE SPECIES AND SUBSPECIES

1. Elytra partly or wholly black or blue-black, at least darker than head and pronotum ..... 2  
    Elytra of same colour as head and pronotum, or lighter ..... 4
2. Glabrous triangles of antennal segments 5-10 coarsely punctured, eyes relatively small, not prominent, elytra entirely blue-black, pronotum relatively large, elytral striae deep and narrow ..... *nigripennis* Dejean  
    Glabrous triangles of antennal segments 5-10 not coarsely punctured, almost smooth, eyes relatively prominent, pronotum average, colour of elytra varying from entirely black to apical  $\frac{1}{2}$  black, elytral striae variable ..... 3

Fig. 23, pronotum, *H. nigripennis*, Clayton, Ga.; fig. 24, *H. ferrugineus*, Austin, Tex.; fig. 25, *H. p. praecustus*, Mt. Vernon, Ala.; fig. 26, *H. p. bicolor*, Wellesley, Mass.; fig. 27, *H. p. floridanus*, Type, Ormond, Fla.; fig. 28, *H. texanus*, Kingsville, Tex.; fig. 29, *H. latitarsis*, Huachuca Mts., Ariz.; fig. 30, *H. clairvillei*, "Florida"; fig. 31, *H. papago*, Huachuca Mts., Ariz.



3. Antennal segments 5-10 varying from slightly wider than long to slightly longer than wide (seg.6-L/W: 0.91-1.16); elytral striae relatively broad ..... *praecustus praecustus* Dejean  
 Antennal segments 5-10 distinctly wider than long, transverse, (seg.6-L/W: 0.57-0.91), elytral striae somewhat narrow ..... *praecustus bicolor* Harris
4. Pronotum appearing long and slender (L/W.base 1.18-1.32), elytra lighter in colour than head and pronotum ..... *clairvillei* Dejean  
 Pronotum not appearing long and slender (L/W.base usually less than 1.18), elytra of same colour as head and pronotum ..... 5
5. Elytral punctation very sparse, punctures tending to be arranged in discrete pairs, elytral striae very shallow, intervals broad, punctation of head and pronotum fine, terminal segment of maxillary palpus broad .... *papago* Casey  
 Elytral punctation variable, but always denser than above, punctures never tending to be arranged in discrete pairs, terminal segment of maxillary palpus variable ..... 6
6. Antennal segments 5-10 relatively broad, longer than wide, as long as wide, or distinctly wider than long (see Figs. 5-8 and 10), sclerotized strips of median lobe slender or broad at base ..... 7  
 Antennal segments 5-10 relatively slender, as long or distinctly longer than wide (see Figs. 2-5), median lobe slender, sclerotized strips slender at base ..... 9
7. Sclerotized strips of median lobe narrow at base (see Fig. 17b), antennal segments 5-10 as long or distinctly longer than wide, punctation of elytral striae triseriate ..... *praecustus floridanus*, new subspecies  
 Sclerotized strips of median lobe broad at base (see Figs. 18b and 19b), antennal segments 5-10 as wide or wider than long, elytral punctation either distinctly biseriate, or tending to be triseriate ..... 8
8. Basal angles of hind tarsal segments broad (see Fig. 22), sides of second and third segments parallel or almost parallel, terminal segment of maxillary palpus very broad, elytral punctation fine, tending to be triseriate, ventral surface of median lobe strongly sinuate in lateral aspect (see Fig. 19a) ..... *latitarsis* Casey  
 Basal angles of hind tarsal segments not broad, sides of second and third tarsal segments tapering from base to apex (see Fig. 21), terminal segment of maxillary palpus not as broad as in *latitarsis*, elytral punctation variable, biseriate in most individuals, but confused and triseriate in some, ventral surface of median lobe not as strongly sinuate as above (see Fig. 18a) ..... *texanus* Le Conte
9. Apical portion of median lobe relatively broad in dorsal aspect (see Fig. 17b), apex not appearing long and slender in lateral aspect (see Fig. 17a), total length 15.4-18.4mm., antennal segments 5-10 longer than wide, elytral striae broad, densely and approximately triseriately punctured ..... *praecustus floridanus* new subspecies  
 Apex of median lobe relatively slender in dorsal aspect, long and slender in lateral aspect (see Figs. 16a and z); length 12.2-16.0mm., antennal segments 5-10 variable, but usually not wider than long *ferrugineus* Le Conte

**Helluomorphoides nigripennis** (Dejean)

(Figures 1, 15, 23)

*Helluo nigripennis* Dejean, 1831: 408*Helluomorpha nigripennis* Castelnau, 1834: 52. Ibid, 1840: 47. Le Conte, 1879: 60.

The relatively small eyes, blue-black elytra with narrow, biserially punctured striae, will serve readily to distinguish this species from all other known North American helluonines. The shape, and relatively large size of the pronotum, and the shape of the maxillary palpi are also of diagnostic value.

*Description.*—The measurements presented below are based on a series of 16 specimens. Length 9.0-11.1-14.0 mm., width 3.2-3.6-4.6 mm. Colour reddish-brown, except elytra which are blue-black, surfaces shining.

Head with vertex and front glabrous, shining, finely and somewhat sparsely punctate above eyes and along posterior margin. Terminal segment of maxillary palpus short, broadening distinctly from base almost to apex, then constricted very slightly, only slightly depressed. Antennae (Fig. 1): segment 4 slightly compressed, coarsely and densely punctate; segments 5-10 with glabrous areas coarsely and densely punctate, segment 6 L/W 0.71-0.87-1.00.

Pronotum as in Fig. 23, relatively large for genus, L/W.base 1.04-1.09-1.16, coarsely and sparsely punctate along margins and median longitudinal impression, irregular elongate areas on disc impunctate, shining; median longitudinal impression broad and deep. Hind tarsi slender, segments almost triangular, tapering strongly from apex to base.

Elytra with intervals high and rounded, striae narrow, biserially punctate. Median lobe of male as in Figs. 15a-b.

*Type and Distribution.*—Lindroth (1955: 25) reports that no example of this species in the Oberthür Collection is marked as a Dejean type. No type locality other than "Amerique septentrionale" was indicated in the original description. The type specimen was sent to Dejean by Le Conte, and was therefore probably collected in southern Georgia, or southern New Jersey. This species appears to be confined to the Atlantic and Gulf coastal plain and piedmont, ranging eastward to Georgia from Texas, and northward as far as Massachusetts. It has not been reported from Florida. Life zones: Lower and Upper Austral. See Fig. 33.

25 specimens have been examined.

**Helluomorphoides ferrugineus** (Le Conte)

(Figures 2, 3, 4, 12, 13, 14, 16, 24, 32)

*Helluomorpha ferruginea* Le Conte, 1853: 373. Ibid, 1879: 60. Horn, 1881: t.9, fig. 103. Heyne-Taschenberg; 1908: 14.*Helluomorpha languida* Casey, 1913: 90.

The slender antennae, slender terminal segment of the maxillary palpus and the relatively broad and shallow elytral striae serve to



distinguish this species from the other members of the genus. *H. ferrugineus* can be most readily confused with *texanus*, but in the greater part of the area where the two are sympatric the discal elytral striae of the former are triseriately punctate, whereas those of the latter are biseriately punctate.

*Geographical variation.*—Specimens of this species which occur on the Atlantic Coast westward to the Edwards Plateau in Texas invariably have the elytral striae triseriately punctate. To the south and west, the elytral punctures are usually finer and less numerous, and in some specimens are arranged biserially. This persists across northern Mexico, and into southern Arizona and New Mexico. The type specimen of *Helluomorpha languida* (Brownsville, Texas) falls in the latter category. The western Texas sample (Fort Davis-Chisos Mountains-Alpine) seems to be intermediate between the two poorly defined conditions.

Specimens from southern Arizona seem to have relatively narrow pronota. To show this, the value of the width of the pronotum was divided by the value of the width of antennal segment 6 for each specimen. The results are presented in Fig. 32. Standard deviations and standard errors were calculated only for samples of 10 or more specimens. These data seem to indicate that while the central Texas ("Texas" and Boerne) and southern Arizona samples are reasonably clearly differentiated, the difference is bridged by the geographically intermediate samples.

Three courses of action seem possible in the light of the data presented above. 1. The species *ferrugineus* may be divided into three subspecies: an eastern one (typical), to include specimens from the Edwards Plateau area, and eastward; characterized by larger elytral punctures, and greater average pronotal width; a southern Arizona race, smaller and fewer punctures on the elytral striae, and a narrower pronotum; and a central-southern race (*languidus* Casey), with average pronotal width intermediate between the other two races, and elytral punctuation like that of the Arizona race. 2. *H. ferrugineus* could be divided into an eastern and western race, with specimens from Mexico and southern Texas being regarded as intergrades. 3. This species would not necessarily have to be divided. I prefer the third alternative because the punctuation character is vague, and there is extensive overlap in relative width of the pronotum from sample to sample. Those wishing to apply a subspecific name to the southern Texas specimens may use *languidus* Casey. Then, specimens from the Edwards Plateau and eastward may be referred to *ferrugineus* (*s. str.*).

*Description.*—Measurements are based on a series of 132 specimens. Length 12.2-13.7-16.0 mm., width 4.4-4.9-9-5.8 mm. Colour uniformly reddish brown, some specimens slightly darker.

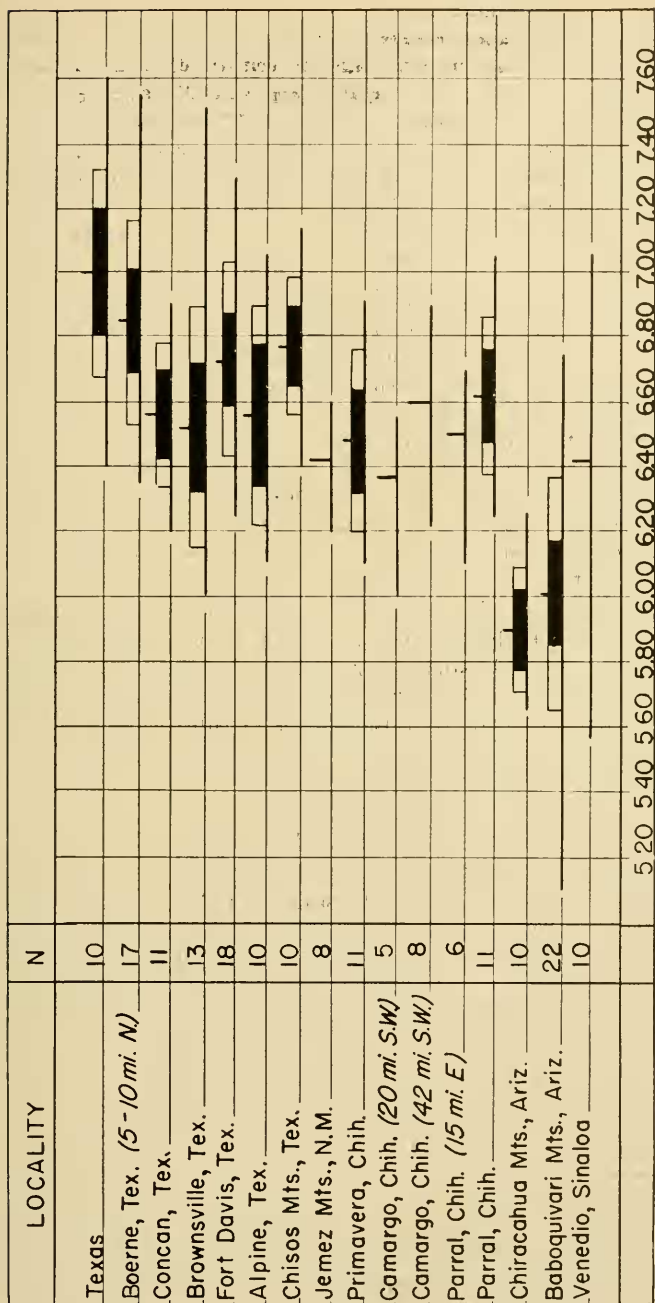


Fig. 32. Variation from east to west in the ratio *W.pn./W.ant.seg.6* in samples of *H. ferrugineus*. Range of variation is represented by the heavy black horizontal line; mean by the short, heavy, vertical lines. The blackened part of each bar represents 2 standard errors of the mean on either side of *M*. One-half of each black bar plus the white bar at either end represent 1 standard deviation on either side of the mean.

Head finely and evenly punctate. Terminal segment of maxillary palpus slender, not widening from base to apex, depressed. Antennae (Figs. 2-4): segment 4 irregularly and somewhat finely punctate, slightly compressed, slender, widening only slightly from base to apex, not triangular; segments 5-10 as long or longer than wide, relatively slender, compressed; segment 6 L/W. 1.00-1.12-1.39.

Pronotum as in Fig. 24, L/W.base 0.93-1.01-1.11, coarsely and densely punctate excepting a narrow longitudinal area each side of median longitudinal impression. Median longitudinal impression broad, shallow, and punctate.

Elytra with striae broad, punctuation variable, as noted in preceding section. Median lobe of male genitalia as in Figs. 16a-b.

*Notes on types.*—The type of *ferrugineus* Le Conte (sex undetermined) is in the Le Conte collection, MCZ No. 5838, and was collected in "Texas." The punctuation of the elytral striae and proportions of the pronotum suggest that this specimen was taken in the eastern part of Texas. *H. languidus* Casey is represented in the Casey collection, USNM No. 47589 by the type and three paratypes, all of which were taken at Brownsville, Texas. As the external diagnostic characteristics of *languidus* grade into those of typical *ferrugineus*, and as the male genitalia of specimens referable to *languidus* are the same as those of typical *ferrugineus*, I feel certain that these two forms are conspecific.

*Distribution.*—This species ranges from Sinaloa, Mexico and southern Arizona, eastward along the Gulf Coast to the Atlantic Coast, and northward to central North Carolina, and possibly to southern New York; northward in the Great Plains to northeastern Kansas. Life Zones: Upper Sonoran to Lower, and possibly Upper Austral. See Fig. 34.

385 specimens have been examined.

#### ***Helluomorphoides praeustus* (Dejean)**

*Helluomorphoides bicolor* Harris is treated as a subspecies of *praeustus* because the geographical ranges of the two forms are complementary, and the diagnostic features form an almost continuous series of variation. The genitalia of the two forms are identical.

The diagnostic features lie in the shape of the median lobe of the male genitalia (Figs. 17a-b), and in the shape of the pronotum (Fig. 25).

#### ***Helluomorphoides praeustus praeustus* (Dejean)**

(Figures 6, 17, 25)

*Helluo praeustus* Dejean, 1825: 289

*Helluomorpha praeusta* Castelnau, 1834: 52. Ibid, 1840: 47. Le Conte, 1879: 61.

The black elytra, prominent eyes, proportions of the antennal segments, and relatively broad elytral striae will separate this subspecies from other forms of the genus.

*Description.*—Measurements are based on a series of six specimens. Length 15.3-16.2-18.8 mm., width 5.0-5.6-7.0 mm. Colour: head, thorax, and basal  $\frac{1}{2}$ - $\frac{1}{4}$  of elytra reddish-brown, rest of elytra black; abdomen blackish-brown, excepting lateral margins and apices of each segment, which are reddish-brown.

Head finely and sparsely punctate, vertex and front impunctate. Terminal segment of maxillary palpus widening slightly from base to apex, relatively broad. Antennae (Fig. 6): segment 4 slightly wider at apex than at base; segments 5-10 more or less quadrate, segment 6 L/W. 0.91-1.01-1.16.

Pronotum as in Fig. 25, coarsely and somewhat sparsely punctate excepting a narrow longitudinal strip each side of median longitudinal impression; this impression broad and deep, sparsely and coarsely punctate. Tarsi slightly darker than pronotum, segments of hind tarsus average in shape and proportions.

Elytra with striae broad, rather finely and densely punctate, the punctures more or less triseriate in arrangement. Median lobe of male genitalia as in Figs. 17a-b.

*Type and distribution.*—The type, which has not been examined in this study, is in the Dejean collection (Rene Oberthur Collection), and is said by Lindroth (1955: 25) to differ from *bicolor* in that the segments of the flagellum are narrower. It was collected in "Amerique septentrionale," probably in southern Georgia or New Jersey, as it was sent to Dejean by LeConte.

The range of this subspecies is poorly known. Blatchley (1910: 155) notes that it is recorded from Cincinnati, Ohio, but I have seen specimens only from Alabama and New Jersey. It would seem that this form is found on the Gulf and Atlantic coastal plain and piedmont and in the Mississippi basin, ranging northward on the Atlantic coast to southern New Jersey, and in the Mississippi basin to southwestern Ohio. This subspecies has been recorded from Sand Point and Tampa, Florida by Leng (1915: 589). Life Zones: Lower and Upper Austral. See Fig. 34.

#### ***Helluomorphaeides praeustus bicolor* (Harris)**

(Figures 7, 26)

*Zuphium bicolor* Harris, 1828: 117.

*Helluo laticornis* Dejean, 1831: 407.

*Helluomorpha pubescens* Klug, 1834: 77.

*Helluomorpha bicolor* Le Conte, 1879: 61.

A combination of dark coloured elytra and transverse flagellar segments are sufficient to distinguish this subspecies from the other North American *Helluomorphaeides*.

*Description.*—Measurements are based on a series of 33 specimens. Length 12.0-14.0-16.6 mm., width 3.4-4.9-6.0 mm. Colour: head, thorax, and basal  $\frac{1}{4}$  of elytra reddish brown, in most specimens, some, however, with elytra entirely black, teneral specimens with elytra entirely reddish brown, abdomen coloured as in the typical race.

Punctuation of head as in typical subspecies. Terminal segment of maxillary palpus as in typical subspecies. Antennae (Fig. 7): segment 4 as in *p. praeustus*; segments 5-10 transverse, segment 6 L/W. 0.57-0.75-0.91.

Pronotum as in Fig. 26, L/W.base 1.00-1.04±1.19, punctation as in typical subspecies. Elytral striae narrower than in *p. praeustus*, densely and confusedly punctate. Median lobe of male genitalia as in typical subspecies.

*Notes on synonymy.*—The synonymy of *bicolor* was presented by Le Conte (1879). I have not seen the types of *laticornis* or *pubescens*, but their descriptions seem to fit *bicolor*.

*Type and distribution.*—The type is a male, in the T. W. Harris Collection at the Museum of Comparative Zoology, MCZ No. 28191.

There is also one paratype, sex undetermined, in the same collection, MCZ No. 28192. They have been examined in this study. The type locality, as given in the original description, is the "Vicinity of Salem," Essex County, Massachusetts.

This is the northernmost race of *praeustus* ranging westward from the east coast to the western edge of the Great Plains, northward to southeastern South Dakota and southern Michigan, southward to central Kansas and Missouri (recorded from Vigo, Posey, and Crawford counties by Blatchley, 1910: 156); on the East Coast, northward to northeastern Massachusetts, southward at least to northern Virginia, and probably as far as Georgia (Fattig: 1949). Life Zones: Upper Austral and Upper Sonoran. See Fig. 34.

A total of 98 specimens representing this subspecies have been examined in this study.

#### **Helluomorhoides praeustus floridanus**, new subspecies

(Figures 5, 27)

This subspecies can be distinguished from the other two races of *praeustus* by the concolorous elytra, and from *ferrugineus* by its larger size, broader elytral striae, somewhat broader maxillary palpi, and by the structure of the male genitalia. Although the antennal segments resemble somewhat those of *texanus* in that they are relatively broad, these two forms can be distinguished by the punctation of the elytral striae: biseriate in *texanus*, and triseriate or dense and confused in *floridanus*. The tarsal segments are relatively longer than are those of *texanus* and the posterior sinuation of the pronotum is much less pronounced. *H.p. floridanus* can be distinguished from *clairvillei* by its broader, more densely punctate elytral striae, and relatively broader pronotum.

*Description.*—Type, male, length 16.6 mm., width 5.8 mm. Colour uniform reddish brown.

Head finely, rather densely punctate. Terminal segment of maxillary palpus rather broad. Antennae (Fig. 5): segment 4 moderately compressed, slightly wider at apex than at base; segments 5-10 longer than wide, segment 6 L/W 1.12, glabrous triangles faintly indicated.

Pronotum as in Fig. 27, L/W.base 1.07, coarsely and densely punctate, especially along lateral margins; median longitudinal impression punctate, a narrow medial area each side of this impunctate.



Elytral striae very broad, rather densely punctate, punctation approximately triseriate. Median lobe of male genitalia as in *p. praecustus*.

Allotype, female, length 17.8 mm., width 6.4 mm. Colour slightly darker than that of type. Terminal segment of maxillary palpus relatively slender, but broader than that of *ferrugineus*. Antennal segment 6 L/W 1.08. Pronotum relatively broader than that of type, posterior sinuation of lateral margins more pronounced, L/W.base 1.06. Elytral striae as in type, punctation dense, not as distinctly triseriate as in type.

Paratypes, 4 males and 2 sex undetermined, length 15.4-17.4-18.4 mm., width 5.0 6.0-6.4 mm. Colour same as type. Terminal segment of maxillary palpus with about same proportions as that of allotype. Antennal segment 6 L/W 1.08-1.10-1.15. Pronotum with posterior incurving of lateral margins variable, from relatively slight to as pronounced as in allotype, L/W.base 1.03-1.05-1.10. Elytra exhibiting slight variation in width of striae, these broad and generally densely punctate, the punctation approximately triseriate. Median lobe of male genitalia same as that of type.

*Types and distribution.*—All specimens are from the northeastern portion of peninsular Florida. They have been returned to the museums from which they were borrowed. The type locality is Ormond, Volusia County, Florida. Leng's Florida record of *ferruginea* (1915: 589) probably refers to this subspecies. Life Zone: Lower Austral. See Fig. 34.

Type, male—Volusia County, Ormond, Feb. 24, 1899, W.S.B. coll., Wickham Coll., 1933, [U.S. Nat'l. Museum]. Allotype, female, Volusia County, De Leon Springs, 7.5.29, John George Gehring coll., [Museum Comparative Zool.]. Paratypes—Volusia County: one male, De Leon Springs, [Museum Comparative Zool.]; Duval County: one male, Jacksonville, [Cornell Univ.]. St. Johns County: one sex undet., St. Augustine, [Calif. Acad. Sci.]. "Fla.": one, abdomen missing, [Museum Comparative Zool.]; one, male, [U.S. Nat'l. Museum].

*Relationships of praecustus.*—Le Conte (1853) noted in his description of *ferrugineus* that "except by the form of the antennae, this species almost exactly resembles *H. praecusta* and *laticornis*; the thorax is, however, less narrowed posteriorly." However, an inspection of the range of variability of antennal segment 6 shows that *bicolor* (*laticornis*) forms a continuous series with *praecustus* and *floridanus*, and *floridanus* and *ferrugineus* overlap 100 per cent with regard to this character. The shape of the pronotum is also sufficiently variable so that it does not constitute an absolute criterion for distinguishing between the two species, since the pronotum of *p. floridanus* resembles in shape the pronota of the Arizona specimens of *ferrugineus*. The partially black elytra will distinguish *p. praecustus* and *p. bicolor* from *ferrugineus*, but the elytra of *p. floridanus* have no black pigment, and therefore resemble those of *ferrugineus*. The elytral striae of *p. bicolor* are relatively narrow, while those of *p. praecustus* and *p. floridanus* are wider and densely punctate as in *ferrugineus*. There is also

a slight difference in the shape of the median lobe which distinguishes all of the races of *praeustus* from *ferrugineus*. From these data it may be seen that *ferrugineus* and *praeustus* are really not very different, and that of the races of *praeustus floridanus* is the one that is most similar to *ferrugineus*.

To a certain extent, these species replace one another geographically. I have seen three specimens of *ferrugineus* from localities within the presumed range of *praeustus*. Of five specimens from Pottawattomic County, Kansas, four were typical *p. bicolor*, and the fifth typical *ferrugineus*. The specimens of *ferrugineus* from Southern Pines, North Carolina, were typical for that species. These data suggest that *ferrugineus* and *praeustus* do not interbreed, and thus may be considered to be specifically distinct.

***Helluomorphoides texanus* (Le Conte)**

(Figures 8, 18, 31, 28)

*Helluomorpha texana* Le Conte, 1853: 374. *Ibid*, 1879: 61.

The following combination of characters separates this species from other members of the genus: colour uniformly reddish brown, antennal segments 5-10 usually slightly wider than long, pronotum wider than long, discal striae of elytra biserially punctate.

*Description*.—Measurements are based on a series of 65 specimens chosen at random from localities throughout the range of the species. Length 13.8-15.6-17.3 mm., width 4.8-5.5-6.2 mm. Colour uniform reddish-brown, darker in some specimens.

Punctuation of head fine and dense, especially in postero-lateral areas, vertex impunctate with exception of line of punctures across middle. Terminal segment of maxillary palpus slightly but noticeably broader than that of *ferrugineus*, decidedly narrower than that of *latitarsis*. Antennae (Fig. 8): segment 4 somewhat compressed, approximately triangular in outline, somewhat coarsely and irregularly punctate; segments 5-10 relatively broad, averaging quadrate, segment 6 L/W 0.73-0.89-1.07.

Pronotum as in Fig. 28, L/Wbase 0.86-1.00-1.20, somewhat coarsely and densely punctate excepting narrow longitudinal area of disc each side of densely punctate median longitudinal impression; median longitudinal impression broad and shallow. Basal angles of hind tarsal segments narrow, sides not parallel, (see Fig. 21).

Discal elytral striae broad, punctuation somewhat coarse, typically biserial, but confused and triserial in a few individuals. Median lobe of male genitalia as in Figs. 18a-b.

*Type and Distribution*.—The type specimen, which I examined, is a male, in the Le Conte Collection, MCZ No. 5837. The type locality is "Texas."

This species ranges from east of the Davis Mountains, Texas, and probably east of the Sierra Madre Occidentale in northern Mexico, northward in the Great Plains to southern Colorado and Kansas, and

possibly Indiana (Blatchley, 1910: 156); on the Gulf Coast as far east as Alabama, and possibly Georgia (Fattig: 1949); not known from peninsular Florida. Life Zones: Upper Sonoran, and Lower and Upper Austral. See Fig. 33.

I have seen 150 specimens of this species.

**Helluomorphoides latitarsis** (Casey)

(Figures 10, 19, 22, 29)

*Helluomorpha latitarsis* Casey, 1913: 189.

The broad basal angles of the hind tarsal segments and the broad terminal segment of the maxillary palpus are the distinctive features of this species.

*Description.*—Measurements are based on a series of 39 specimens, except as noted below. Length 13.5-15.9-17.9 mm., width 4.6-5.8-6.4 mm. Colour uniform reddish-brown. Very similar in general proportions and appearance to *texanus* Le Conte.

Punctation generally finer than in *texanus*, head finely, densely, and evenly punctate. Terminal segment of maxillary palpus appearing very broad, lateral margins parallel. Antennae as in *texanus*, but averaging somewhat narrower (see discussion below, and Fig. 10).

Pronotum as in Fig. 29, L/W.base 0.94-1.05-1.13, posterior sinuation of lateral margins usually more pronounced than in *texanus*. Segments of hind tarsus with broad basal angles, sides parallel, and apical setae on each segment shorter than in *texanus* (see Fig. 22).

Elytral striae broad, punctures fine, typically confused, but biseriate in a few individuals. Median lobe of male genitalia generally as in *texanus* but with apex slightly longer and more slender, and ventral surface more strongly sinuate. See Figs. 192a-b.

*Geographical Variation.*—For purposes of this study, three samples are considered in some detail: one, from the Baboquivari Mountains of southern Arizona, is typical of specimens found in that state; a second is a composite sample from several localities in Chihuahua, Mexico; the third consists of specimens collected at Fort Davis, Texas. Mensural data for a sample of seven specimens from Alpine, Texas have been lost and therefore cannot be presented. However, this sample was very similar to the Fort Davis Sample in the characters noted below. See table I for data on variation in proportions of antennal segment 6.

These data were not analyzed statistically because their distributions did not seem to fit the normal curve of error (except the Baboquivari sample), and so a frequency distribution seemed the best way to present them. A trend in the flagellar segments from wider than long to longer than wide seems to be indicated, with the geographically extreme samples being morphologically extreme.

Table I. *Helluomorhoides latitarsis*: Frequency Distribution of Values for the Ratio Antennal Segment 6 L/W.

Values	Localities		
	Baboquivari Mts., Ariz.	Chihuahua, Mex.	Fort Davis, Tex.
0.75-0.79	2	1	
0.80-0.84	4	2	
0.85-0.89	5	2	1
0.90-0.94	3		1
0.95-0.99	1		2
1.00-1.04		6	3
1.05-1.09		2	1
1.10-1.14			6
1.15-1.19			1
N	15	13	15
Mean	0.87	0.97	1.04

The basal angles of the hind tarsal segments (especially segment 3) seem to be somewhat narrower and the segments appear to be slightly longer in the Fort Davis specimens than in the Mexican or Arizona samples. However, the angles are definitely broader than are those of *texanus*.

The elytral striae of the Fort Davis specimens are usually biserially punctate, whereas the usual (but not universal) condition in the Mexican and Arizona samples is that the arrangement of punctures is more confused.

Thus it may be seen that the Fort Davis sample differs slightly from specimens occurring over the rest of the range of *latitarsis*. Further, the Fort Davis sample approaches *texanus* in elytral punctuation and structure of the hind tarsal segments. (However, the male genitalia and terminal segment of the maxillary palpus are typical for *latitarsis* in this sample.). Originally, I interpreted this as evidence that the Fort Davis sample represented an intermediate population between *texanus* and *latitarsis*, but I now think that this view is incorrect, and that the two named forms though very similar morphologically, and apparently completely allopatric, are actually distinct species. However, the possibility that the Fort Davis, and presumably the West Texas population of *latitarsis* is of hybrid origin must be borne in mind, and deserves further investigation.

*Type and Distribution.*—The type is a male, in the Casey Collection, USNM No. 47590. "Arizona" is the only locality given in the original description, and so specimens collected in Arizona are typical from a nomenclatural point of view. I have seen and dissected the type.

This species ranges from western Texas to southern Arizona, as far north as Globe; southward on the Mexican Plateau at least to the state of Durango. See Fig. 33.

I have seen 74 specimens of this species.

**Helluomorphoides clairvillei** (Dejean)

(Figures 9, 30)

*Helluo clairvillei* Dejean, 1831: 406.*Helluomorpha clairvillei* Castelman, 1934: 52. Le Conte, 1879: 60.

A combination of large size, relatively broad flagellar segments, pronotum relatively elongate with narrow base, and head and prothorax darker in colour than elytra and abdomen, distinguishes this species from other North American helluonines.

*Description*.—Measurements are based on a series of 11 specimens. Length 16.0-18.4-21.0 mm., width 4.8-5.5-6.2 mm. Colour reddish-brown, head, prothorax and tarsi darker brown.

Head rather finely and densely punctate along lateral and basal margins, vertex impunctate. Terminal segment of maxillary palpus relatively narrow at base, broadening slightly to apex. Antennae (Fig. 9): segment 4 somewhat compressed, triangular in shape and densely punctate; segments 5-10 wider than long, compressed, segment 6 L/W 0.71-0.83-0.93.

Pronotum as in Fig. 30, L/W.base 1.18-1.25-1.32, coarsely and somewhat densely punctate along margins, and along the deep and broad median longitudinal impression; disc coarsely but less densely punctate than lateral areas. Hind tarsus, segment 3, widening only slightly from base to apex.

Elytra with intervals well defined, broad and rounded, striae each with two rows of punctures. Median lobe of the male genitalia as in *texanus*.

*Type and Distribution*.—Concerning the type, which is in the Dejean Collection Lindroth (1955:25) states: "*Helluo clairvillei* = *Helluomorpha clairvillei* auct. Compared with a male from Lucedale, Mississippi." I have seen the latter specimen. The type was collected by Escher in "Amerique septentrionale."

This species ranges on the Gulf and Atlantic coastal plains and piedmont from eastern Mississippi to central Florida, and northward to southern New Jersey. Life Zone: Lower Austral. See Fig. 33.

*Notes*.—This species seems to be closely related to *texanus* Le Conte, resembling that species in relative proportions of the antennal segments, shape of the median lobe of the male genitalia, and punctation of the elytral striae. Possibly *clairvillei* and *texanus* are subspecies, because the two forms to a large extent replace one another geographically. However, their ranges overlap in Mississippi, Alabama, and Georgia, and no intergrade specimens have been seen from this area. If the effects of the genetic factors determining shape and colour of the pronotum were essentially discontinuous, and if these were determined by a single pair of alleles, then morphological intergrades would not be expected, even though the two forms were capable of interbreeding. No genetic data are available, so it seems best to go on what is indicated by the morphological evidence.

A total of 18 specimens of this species have been examined.



***Helluomorphoides papago* (Casey)**

(Figures 11, 20, 31)

*Helluomorpha papago* Casey, 1913: 190.

The outstanding characters of this species are the fineness and sparseness of the elytral punctation, the shallow elytral striae, and the broad terminal segment of the maxillary palpus. In most specimens the elytral punctures are arranged in discrete groups of two.

*Description*.—Measurements are based on a series of 10 specimens. Length 11.5-13.1-14.5 mm., width 4.0-4.5-5.2 mm. Colour uniformly reddish-brown.

Head shining, generally finely and somewhat sparsely punctate. Terminal segment of maxillary palpus broad, lateral margins parallel, as in *latitarsis*. Antennae (Fig. 11): segment 4 slightly broader at apex than at base; segments 5-10 varying from slightly wider than long to slightly longer than wide, relatively slender, as in *ferrugineus*, segment 6 L/W 0.93-1.03-1.27.

Pronotum as in Fig. 31, L/W.base 1.00-1.03-1.14, finely and sparsely punctate along margins, median longitudinal impression broad, shallow, punctation in general fine.

Elytra with intervals broad, shining, slightly elevated, striae each with a double row of a few fine punctures which are arranged more or less in discrete pairs. Median lobe of male genitalia as in Figs. 20a-b.

*Type and Distribution*.—The type, which has been examined in this study, is a male, in the Casey Collection, USNM No. 47588. The type locality is "southern Arizona." This species is found on the Mexican Plateau, ranging northward from San Juan del Rio, Durango, Mexico, to the mountains of southern Arizona, and eastward to the Davis Mountains, Jeff Davis County, Texas. Life Zone: Upper Sonoran.

A total of 28 specimens have been examined in this study.

## RELATIONSHIPS OF THE SPECIES

At this time it is impossible to consider more than the relationships of the North American species of *Helluomorphoides* to one another. These seven species can be arranged in four groups. 1. *H. nigripennis* is the most distinctive, and in some ways seems to be closer morphologically to the South American species than to the other forms which enter North America. 2. *H. ferrugineus* and *praeustus* seem to constitute a second group, as the two are closer to one another morphologically than either is to any other species. There seems to be a trend toward broadened flagellar segments within this group, and using this character as a criterion of degree of specialization, *ferrugineus* would be regarded as the more generalized of the two species and *p. bicolor* as the most specialized race of *praeustus*. 3. A third group includes *latitarsis*, *texanus* and *clairvillei*. Of these three species, *texanus* seems to be the least derivative, being average in proportions of the palpi, tarsal segments, and pronotum. *H. latitarsis* is derivative in

proportions of the palpal and tarsal segments but is generalized in proportions of the flagellar segments, and of the pronotum, and *clairvillei* is derivative in colour pattern and proportions of the pronotum. 4. *H. papago*, like *nigripennis*, stands by itself. The data needed to arrive at an understanding of the relationships of the groups to one another and to the other species of the genus are not available at present.

#### GEOGRAPHICAL DISTRIBUTION

(Figures 33, 34)

The Tribe Helliuonini is discontinuously distributed. It is represented in the Australian Region, southeast Asia, Africa, the Nearctic Region and Central and South America. It is not known to occur in the Palaearctic, nor in the northern portion of the Nearctic Region. From such a pattern of distribution it may be deduced that this group is ancient, and that its dispersal predates the beginning of the Cenozoic Era (Dunn: 1931).

Of the three New World genera, two are restricted to South America. *Helluomorphoides* probably arose in South or Central America and spread northward from there. This seems likely because most of the species of the genus are tropical in distribution. Three of the four species groups which are treated here are found on the Mexican Plateau. Of these, two (*texanus* and *ferrugineus* groups) are represented also in the Great Plains, and in eastern United States. The third group (*papago*) is not known to occur east of the Davis Mountains, Texas. A fourth group (*nigripennis*) is restricted in its distribution to the Gulf and southern Atlantic coastal states.

The exact time and routes of invasion of these groups into North America cannot be known, but judging from the distribution pattern of the recent species it seems likely that the ancestral stocks of *nigripennis* and the *ferrugineus* and *texanus* groups entered the area under consideration in early glacial or late preglacial time. The *nigripennis* stock may have come *via* the coastal plain, if the present distribution of this species means anything in reconstructing its past history. As the remaining species occur in rather dry habitats, even in the basically humid southeast, they probably came northward by way of the Mexican Plateau: *ferrugineus* and *texanus* stocks along the eastern Sierras, and *papago* along the western. The limited distribution of *papago* in North America could mean either that this species is a relatively recent arrival or that it has not been able to move farther west for ecological reasons.

At the time of entry into North America, probably both the *texanus* and *ferrugineus* group stocks were, or became widespread, but probably only in the drier ecological zones (pine forests in the southeast and oak-pinon pine woods in the southwest). The climatic changes of the Pleistocene glacial periods probably caused a fragmentation of the range of these two stocks, resulting in geographical isolation into several more or less southern refugia. The *texanus* stock was proba-

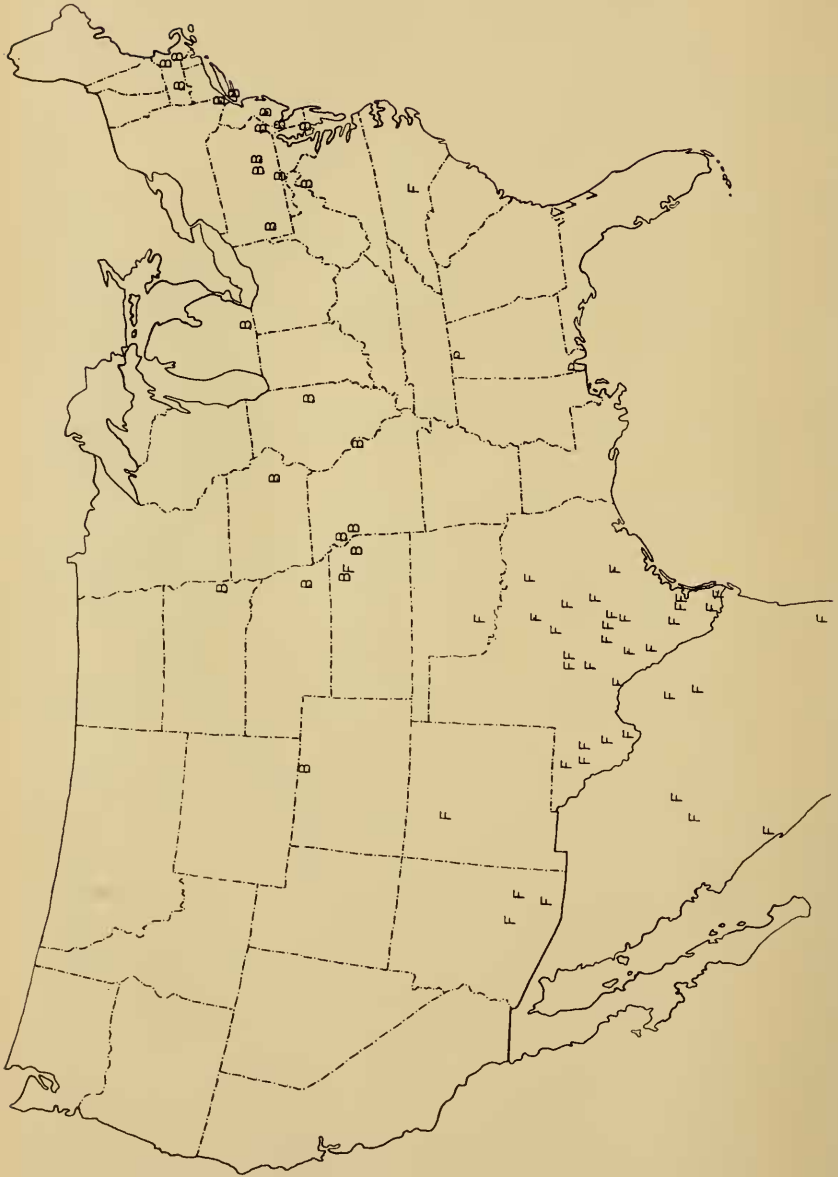


Fig. 33. Map showing the distribution of *H. ferrugineus* and *praenustus*; F, *ferrugineus*; V, *praenustus floridanus*; P, *praenustus praenustus*; B, *praenustus bicolor*.

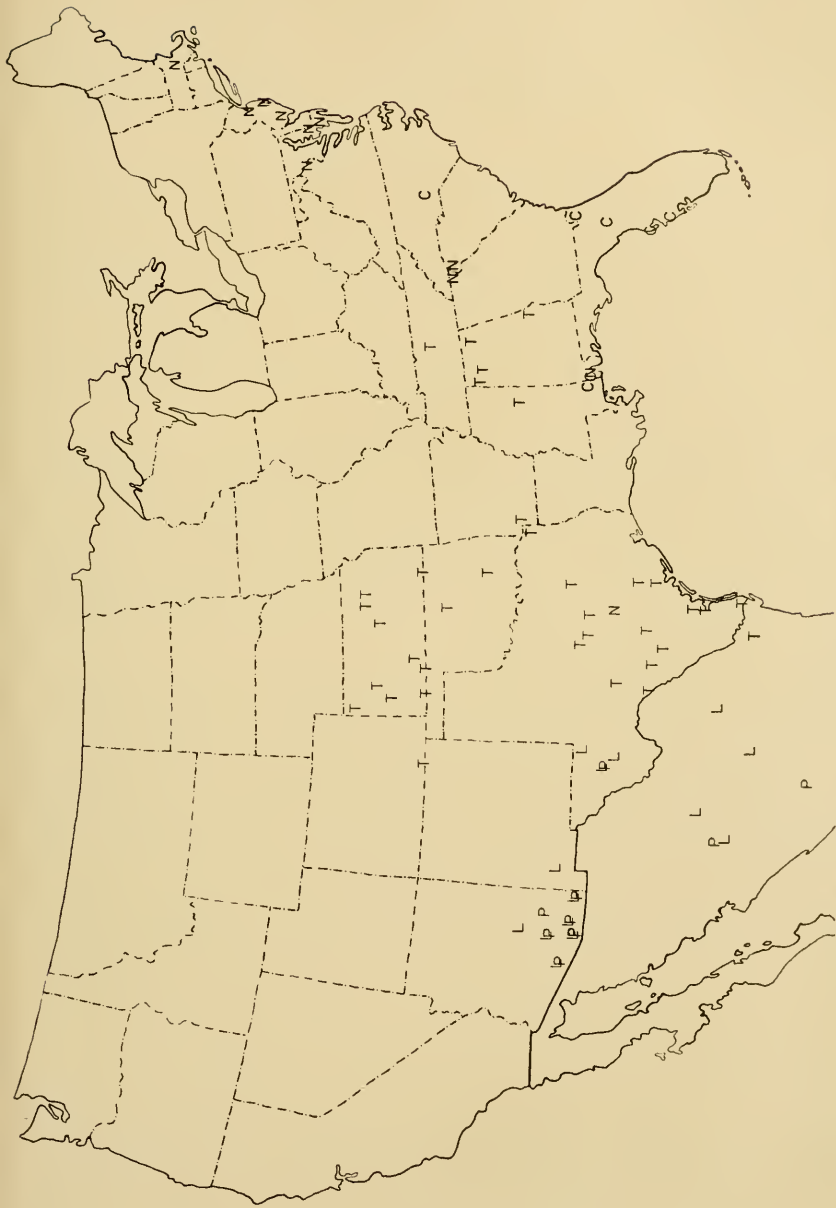


Fig. 34. Map showing the distribution of *H. nigripennis* (N), *clairvillei* (C), *turanus* (T), *latitaris* (L), and *papago* (P). Note: The localities marked on Figs. 33 and 34 are based exclusively on material that I have examined. Records in the literature that I have not been able to verify are not considered.

bly divided into three parts: one in southeastern United States (possibly Florida), one in eastern Mexico, and one in western Mexico. The *ferrugineus* group stock survived in at least two, and possibly all three of the above areas. *H. nigripennis* may have survived the glaciations in either an eastern Mexican or the southeastern refugium, and the *papago* stock was probably restricted to the western Mexican refugium.

During the period or periods of isolation, the *texanus* stock differentiated into three species: *clairvillei* in the southeast, *texanus* in eastern Mexico, and *latitarsis* in western Mexico. The *ferrugineus* stock differentiated into two species: *praeustus* in the southeastern refugium (the least derivative race of this species is Floridian), and *ferrugineus* in Mexico. The slight differentiation of *ferrugineus* in the southwest may mean that this species survived in two Mexican refugia. On the other hand, the differentiation is of such a low level that it could very well have developed in post glacial time, and be correlated with the dispersal of a stock from a single area.

In post glacial time, the species of *Helluomorphoides* spread out from their refugia, eventually attaining their present ranges, and in the process of this dispersal, *praeustus* became differentiated into three geographical races. One peculiarity not accounted for is the distribution of *nigripennis*. This species is known only from United States, and does not seem to have Mexican "roots." This problem may be satisfactorily resolved when the Mexican-Central American species of the genus are worked out.

The hypothesis presented above rests on several assumptions. 1. Speciation in *Helluomorphoides* has come about as a result of fragmentation of once continuously distributed stocks. 2. Fragmentation and isolation of once continuously distributed stocks has occurred. 3. It is possible to predict approximately the location of the refugia postulated above. Assumption 1 rests on the further assumption that geographical isolation is necessary for speciation to occur. I think this may be true at least of terrestrial omnivores, such as most carabids are. The support for assumption 2 and for the existence of southeastern and eastern Mexican refugia is derived from the distribution patterns of other organisms (see Carr, 1940; Beecher, 1949; Hubbell, 1954). I am not aware of any data bearing on a western refugium, but postulate the existence of one on the basis of the present distribution of the *texanus* species group.

This hypothetical history is an outline and probably a gross oversimplification of events that may have led to the development of the recent North American helluonine fauna. It is a series of guesses that seem reasonable in the light of what data are available on the morphology and geographical distribution of the North American species of *Helluomorphoides*, and in the light of what is known about past climatic changes, and about the process of speciation.



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